A PRODROME OF A MEMOIR ON ANIMAL LOCOMOTION.

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The writer has undertaken at the request of the representatives of the University of Pennsylvania a series of studies on animal locomotion. The subject has been approached from the point of view presented by instantaneous photography, and has been especially based on the results obtained by Mr. Eadweard Muybridge. The writer desires in this connection to return his acknowledgments to Mr. Muybridge for opportunities in examining early impressions of the plates, which he is engaged in publishing under the auspices of the University, and also to state that he is indebted to Prof. Thomas Eakins for facilities afforded in studying the results of an experiment in the use of a modified form of Marey's wheel, devised by him in photographing the action of the horse in motion.

This short paper embraces the points which have been thought to have sufficient interest to appear in advance of the final memoir, and will include observations on the movements of the quadrupeds only.

Many of the statements could have been deduced from data already accessible to the writer. But since he wrote the paper immediately after the inspection of the photographs his conclusions may be said to be based upon them. At the same time he has not hesitated to include materials not embraced by the photographs. Whenever practicable the study of a given series was carried on at the same time that the animal itself lay dissected before him. For example, when studying the photographs of the elephant he had the good fortune, through the courtesy of Prof. Huidekoper, to dissect the limbs of an elephant. He has also dissected[1] the horse, the ox, the raccoon, the sloth, the skunk, the Virginian deer and the domestic cat.

THE USE OF TERMS.

It is necessary to propose the use of a few terms which will clearly express in a word a meaning which otherwise would require the employment of a cumbersome phrase. The words flexion, extension

[1] In this connection the writer wishes to give especial acknowledgments to his friends Prof. Horace Jayne and Mr. Edwin A. Kelly.

abduction, adduction, pronation and supination imperfectly express many animal movements. Thus no adequate word exists for the movement of the hand upward and downward when the forearm is held in semipronation. Such a motion is of importance in describing the wing of the bird and the bat. The term *Planation* is here thought to be convenient since it expresses the fact that the movement of the hand is in the plane of the flexor surface of the forearm. Planation includes both pronation and supination. *Contraplanation* as easily indicates a movement at an angle to the plane of the flexor surface of the forearm. It embraces flexion and extension and is not especially demanded, except that a term which includes both flexion extension as well as abduction, as used in the sense of abduction of the thumb, may be acceptable.

In like manner it has been found useful to employ terms for the different orders of the foot-falls.

Synchiry indicates that the right and left foot of a single pair act together. Thus in the gallop the horse moves all the feet synchirally. The movement of the lower limbs in man is also synchiral. The feet may act alternately or together.

Asynchiry would naturally embrace the movements in which the feet act in combinations of hind and forefeet. But since these movements are varied and important, it has been thought desirable to substitute a positive term, and the word *heterochiry* [1] is proposed. The walk, the trot and the rack are heterochiral, since the fore foot is followed, not by its fellow, but by a hind foot. When the hind foot alternates with the fore foot of the same side *lateral heterochiry* occurs. When with the fore foot of one side the hind foot of the opposite side alternates, *diagonal heterochiry* takes place.

In connection with the terms flexion and extension the following will be used:— The movement of a limb against the medium in which the animal is moving constitutes the "*stroke.*" The movement in preparation of the stroke constitutes the "*recover.*" In the description of the "hand over hand" movements of the sloth and the monkey, the word "flexion" has no place; yet the "recover" is used in as exact a sense as in the movements of any other animal.

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[1] While assuming the responsibility for this word the writer desire at the same time to say that it was suggested to him in a conversation with his friend Prof. T. N. Gill.

When a limb of a terrestrial quadruped rests upon the ground it may be said be "on," and when not on the ground, to be "off."

The term "*sura*" will be employed as a convenient word to include the hind limb from the knee to the ankle. "*Crus*" has been retained so generally as a synonym for the entire posterior extremity as not to be available.

"Stroke" is the period of impact. It is included in flexion, and constitutes its first stage. "Recover" embraces the last stage of flexion and the whole of the period of foreward movement. The terms "stroke" and "recover" are by no means the same as flexion and extension. They simply express certain phases of limb-function which are seen during the acts of backward and foreward movements.

THE POSITION OF LIMBS.

In studying the motions of the limb of a vertebrate the position which answers to that taken by the salamander, when at rest, is assumed to be the best adapted for comparison. In this position the limb is horizontal to the plane of the longitudinal axis of the body. The venter of the body and the ventral surface of the limb are on the same plane nearly. The limb of a reptile varies scarcely at all from that just named. When a terrestrial animal is erect the limb instead of being on the same plane with that of the body is moved a quarter of a circle downward. In the bird the posterior extremity when at rest is in the same position as the terrestrial, but the anterior extremity, in marked contrast to it, is flexed. When extended the extremity is thrown upward to a position as far removed from the horizontal position of the salamander in one direction as is that of the terrestrial quadruped in the other.

In the movement of all limbs the directions in the main are forward and backward. Both the movements are oblique but between them is a position which is straight. In the terrestrial animal this position may be said to answer to a line in the anterior extremity which lies immediately in advance of the withers and in the posterior extremity to the centre of the acetabulum.

THE MOVEMENTS OF LIMBS.

If a limb can be conceived moving *in vacuo* it can be at once understood that propulsion is impossible. For propulsion can follow only upon the initiation of an impetus and this in turn only by the resistance of the limb against the medium in which the animal

is moving, or in the case of the terrestrial animal, the surface of the ground.

The resistance of the air and the water are so much less than that of the earth that the acts of flying and of swimming become radically different from those of walking, of running, or of any allied movement. In flying and swimming the resistance made by the limb against the medium in effecting an impetus does not arrest the movement of the pinion or the foot; whereas in terrestrial movements the instant that the foot strikes the earth the resistance is great and the arrest is complete.

In the swimming turtle the first stage of the recover drives the foot in spite of the resistance of the water to the point at which the second stage begins. With some slight modifications the same is true of fossorial animals. Thus in flying, in swimming, and in burrowing the limb describes a continuous movement which unites the path of the stroke to that of the recover. In the animal moving on the surface of the ground, the foot being brought to rest, an absolute break occurs between the beginning of the act of recover and its completion,—the time which would be required to describe the interval and thus to complete the union corresponds to the period that the foot is on the ground. This period constitutes the stroke.

The limb rests on the ground until the trunk moves beyond the point at which it can maintain itself. It is lifted at intervals which are dependent upon the momentum of the moving mass. One, two, or three limbs may be on the ground at the same time. The rates at which the succession of the foot-falls occur, in their turn, depend not only upon the rate of speed at which the animal is moving, but on the gait as well.

KINDS OF WORK DONE BY THE LIMBS.

The kinds of work done by the limbs are two in number, viz., that done by the fore limbs and that done by the hind limbs. The hind limbs are more powerful than the fore limbs, and in some animals, as the kangaroo and the jumping mouse, are the main effectives. No terrestrial animal depends for support upon the fore limbs. When all the limbs are equal or nearly equal in length, the preponderance is still in favor of the hind limbs owing to the fact that the great backward movement of these limbs on the trunk is made possible by the fixation of the bones to the pelvis and through this structure to the vertebral column. Not only is this the case but the hind limbs alone possess the power of propelling the body so as to throw upon the

fore limbs the labor of accommodatiug themselves to the rate of work of their more powerful associates. When an animal is moving at a high rate of speed, as in the gallop, the synchiral action of the hind limbs projects the body with such force as to compel the fore limbs to act simply as props which successively carry the body forwards until one of the hind limbs is again in position to give the body a second impetus. In proof of this assertion it is only necessary to observe that the greatest height attained by the trunk is that secured by the rump when both hind feet are off the ground. The statement generally made that the horse leaves the ground by one of the fore feet creates the impression that he gains the springing force from this foot, all the previous movements being in preparation for such a spring. In place of this statement another is here substituted, viz., that the horse springs from that hind foot which last leaves the ground and is "off" from all feet when he simply relinquishes the support afforded by the last prop, that is to say the last fore foot.

If the fore and hind limbs were based on the same plan the motion of an animal would be either a series of springs—the two feet pushing against the ground at the same moment—or a series of steps, the two feet moving alternately. While closely resembling one another the two limbs are not on the same plan. If any motion takes place in the vertebral column at the time that the fore limb is moving it is noticed that it occurs in the region of the neck. The scapula has a slight motion downward and backward. The motion in the hind limbs occur in the region of the lumbar vertebræ while the pelvic bones are fixed. The limit of the forward motion of the hind limbs is dependent upon the flexibility of the lumbar vertebræ. The limit of the similar motion of the fore limb is determined by the action of the muscles alone. The forward motion of the fore limbs is essentially the same in all animals; but the forward movement of the hind limbs is variable, because the lumbar vertebræ differ in degrees of flexibility. In unguiculates there is more lumbar flexibility than in ungulates. In backward movements the opposite obtains, for in these positions the fore limbs can be carried back to a variable distance. In the deer and its congeners the fore foot can be brought to a point near the centre of the body, and the limb be vertical. In the horse the fore limb in backward strain is very oblique and the foot while well placed under the trunk cannot reach the centre. In the macaque the fore foot cannot pass beyond a vertical line which intersects the trunk a little back of the shoulder-joint. The backward movement of the hind limb is nearly the

same in all animals. The leg is always carried in a direct path, the limit of the movement being determined solely by the length of the limb. In a word the forward movement is the less constrained in the fore limb while the backward movement is the least constrained in the hind limb. The most variable movements are the backward for the fore-limb and the forward for the hind-limb.

The foot in all animals excepting the horse (and even in this single toed form the movement of the foot is nearly all essentials the same) is carried forward in semipronation. The foot strikes the ground on the outer border. Pronation now begins and is completed by the time the perpendicular line is reached. The foot leaves the ground by the inner border (the toes being successively abducted) so that the pressure of the body is borne from without inward across the foot. The foot is always everted as it leaves the ground. In a plantigrade animal, as the raccoon, the foot is carried during the last part of recover nearly parallel to the plane of support. In the rapid motion of ungulates the foot may actually touch the ground nearly to the hock. In backward strain the hock or heel is gradually raised and at the end of strain the animal is seen touching the ground by the tip of the inner functionally active toe. In the horse the foot leaves by the tip of the hoof. It is likely that the degree of impact of the outer border of the foot will be found to correlate with the degree of development of the calcaneo-sural joint* since the weight must be carried along the outer border to the rest of the limb. At the end of backward strain the limb from the knee distally is in the same line. The moment flexion begins eversion is established, and the limb becomes angulated outward at the ankle. The main axis of the proximal facet of the astragalus is correlative with the degree of this obliquity. It is most pronounced in the horse, less so in the ox, and scarcely at all in the hog.

It has been already seen that when the limb is in the position of arrest and the momentum carries the body beyond the perpendicular line it is thrown into "backward strain." The instant that the strain begins the knee is seen to move outward and the hock to move inward. The parts of the foot below the heel remain unchanged. The impact of the structures of the limb are thus impaired in backward strain. It is well known that in the pentadacyle forms the foot can be readily rotated at the medio-tarsal joint and it is a reasonable

*A name proposed for the joint existing Letween the fibular process of the calcaneum and the fibula or the tibia.

assumption that it is at this joint that the distal part of the limb moves when the entire limb rotates outward. The femur, the bones of the leg, and the astragalus act as one factor; and the calcaneum and the remaining bones of the foot as the other factor. The socket for the proximal motion occurs at the hip, and that for the distal at the concavity of the scaphoid bone. There is also considerable motion between the calcaneum and the cuboid bone and between the calcaneum and the lower end of the fibula, if this bone is present, or with the outer end of the tibia if it is absent. Outward rotation of the main portion of the limb carries the calcaneum slightly inward by reason of the articulation between the calcaneum and the bones of the leg, Facets are here present in most terrestrial mammals. In the wombat the articulation is evident. It is present in a rudimentary form in man.

The outer surface of the calcaneum of the bear is marked by a stout roughened ridge as it enters into articulation with the fibula. In the dog the surface is a small embossment which probably is in contact with the fibula only at the time of the backward strain. In a single old dog examined the same ridge is present as in the bear. A similar ridge which developed under the stimulus of diseased action is seen in the skeleton of the tiger in the Museum of the Academy.

As the knee is rotated outward the outer border of the foot is slightly inverted. This disposition is opposed by the peroneus longus muscle which everts the foot. Coincident with the inversion the external crucial ligament becomes tense and the tendency to torsion is checked.

The first movement noticed in the limb after it is beyond the centre of gravity is the flexion of the foot. In the horse the hoof is thrown backward and the under surface of the foot is directed backward, the heel being raised first. The sole is next directed upward. In animals possessing more than one functionally active toe the toes are quickly adducted in the air so as to offer the least resistance to the impetus of the entire body. Associated with the above a pronounced flexion of all parts of the limb occurs excepting at the hip, where the movement is slight. A movement of the thigh toward the trunk is indeed discernible. In animals possessing long thigh-bones, such as the elephant, the movement is more decided than in the ungulates. The same remarks are applicable to the movements of the humerus. The degree to which flexion is carried is more marked in the young than in the adult, and in terrestrial than

in arboreal creatures. In the sloth (*Cholœpus*) flexion is absent, the limbs being advanced by a swinging motion at the shoulder and the hip.

The unaided eye receives the impression of backward movement but fails to be impressed with forward movement. It may hence be inferred that the former is a quicker movement than the latter.

In the fore limb the last state of extension of the forearm answers to the action of the extensors of the carpus and of the digits. In the less delicate movements of the hind limb the muscles which extend the tarsus and the toes move the foot with less precision and it is likely with less speed.

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